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Courtship Behaviors of the Hawaiian Picture-winged *Drosophila*.—Herman T. Spieth. 1984. University of California Publications in Entomology, Vol. 103. vii + 92 pp. $9.50.

The picture-winged species-group members, as implied by their name, are the most impressive Hawaiian Drosophilidae. This is only one of ten species-groups erected for Hawaiian *Drosophila,* but comprises about one-quarter of the species. The group has been a favorite of many evolutionary biologists because of their modifications, which include lekking and very complex courtships. Here Spieth adds to our knowledge an impressive amount of previously ignored behavioral information. Despite what I feel to be major conceptual and some methodological flaws in this publication and in the companion paper (Spieth, 1982), the work is still of lasting significance.

Spieths' work views with work on Hymenoptera sociality as the most thorough behavioral analysis devoted to the study of insect evolutionary relationships. My perusal of the work uncovered 57 behavioral elements (fixed-action-patterns in ethological jargon), 53 of which are employed by the male flies for female sexual stimulation. Some elements are so distinct (i.e., anal droplet pulsation, and the manner of wing semaphoring) that there is little question of their homology in different phases of the same fly's courtship as well as among species. This, and the fact that various combinations of element sequences are performed, makes the taxonomic value of the characters obvious. In fact, Spieth comes to some substantial taxonomic conclusions. For example, the various affinities of *Drosophila neoperkinsi* and of *D. differens* are confirmed by their behaviors. The reluctance to revise the classification of some flies, however, is disconcerting. Four instances are obvious where Spieth is content with *status quo* even though blatant behavioral evidence contradicts the standard taxonomy: *Drosophila picticornis* is deemed a relictual species having affinities with

almost all other members of the whole species-group, but it is kept as a member of the *planitibia* subgroup. Also, *Drosophila conspicua* is kept as a *pilimana* subgroup member even though (p. 57) "it rationally can be considered the founder and at present the sole member of a new, unnamed species-subgroup of the picture-winged flies."

Cladistic practitioners will have plenty to sink their teeth into here. On one hand, the work does appear phylogenetic since hierarchical groups are supported and some even devised, the amount by which they are divided depending on character variability and number. Also, taxon sizes are disparate so as to emphasize relationships (but not entirely, as I mentioned earlier) and not taxonomic convenience. Implicit throughout is a dependence in reconstructing phylogeny not on the discovery of ghost taxa, but of new characters. However, paraphyletic groups are the rule rather than exception, probably because Spieth has a phenomenal assurance in identifying ancestors that is almost eerie. *Drosophila macrothrix,* for instance, is explained as (p. 49) "probably the founder of a new species-group sometime in the future if it should provide immigrants to other islands." The 1982 paper in particular is riddled with very extensive discourse on ancestors and, frankly, all of it is supported by no more explicit reasons than statements like "behavioral and chromosomal evidence indicate that [x] evolved out of [y]." These methods are probably the reason why the characters used to support the existence of the *adiastola* species-subgroup (i.e., hypertrophied male labellar "setae") are also those that define the modified-mouthparts *species-group.* Evolutionary biologists, beware.

Considering the current rage among evolutionary biologists (i.e., Bateson, 1983), it is a boost to know that female choice really does seem to be at work in the cladogenesis of these flies. Of the 71 male courtships that were analyzed, only for 10 of the species were they indistinguishable. Females of most species were found to be passively motionless during courtship and usually responded, if receptive, simply by extruding the oviscape. Most often females were unresponsive to male overtures. Besides the fact that stimulation of the female appears to be the main selection pressure in sexual elaboration, Spieth mentioned on the last page—but provides no data—that most females in nature eventually become mated since most are inseminated. "How much is most?" can be a very important consideration. Based on Spieth's data, I dare say that sexual behavior seems to have evolved much faster than morphology, proteins, the use of larval breeding sites, and even chromosome structure. It is a pity that no mention is made in either publication of recent ideas on directional mate choice in relation to the direction of phylogeny (reviewed in Giddings and Templeton, 1983), a topic introduced by Kaneshiro's work on these very same flies. Other relevant papers that were not addressed are Ringo (1977) and Templeton (1979), as well as several classics.

To really appreciate this work the 1982 paper must be read. This monograph is difficult to wade through since it is 90% species courtship descriptions, with a synthesis of the behavioral, biogeographic, karyotypic, and breeding site information in the 1982 paper. Inexcusable on the part of the author and editors is that most of the review portions of the monograph reiterate, verbatim for some paragraphs, parts of the 1982 paper. Why both publications were not published as one monograph is beyond me. On par for the Hawaiian drosophilidologists, except for D. Elmo Hardy,

is a distressing lack of suitable illustrations. The monograph has only 5 line drawings, all of which are also in the companion paper. Figure 1 is actually quite awkward: it should be labelled as the labellum instead of "mouthparts" for the sake of precision, and is better interpreted when pointing left rather than up. This lineage of flies is certainly among the most bizarre in Acalyptratae Diptera, but the illustrations and morphological interpretations do not bear that out. For instance, the hypertrophied "setae" on the labellum of some species are probably prestomal teeth, which are modifications of the pseudotracheae. The meanings of some terms are vague. Not until page 35 will the reader discover that "HUW" posture mentioned in the previous descriptions is the Head Under Wing posture. Wing "vanes" are the blades; "anal papilla" is the cercus; and the manner of semaphoring (deliberate wing motions, as a flagman makes when signalling) should be made explicit. I suspect that when "drosophiloids" of Hawaii are mentioned, reference is made actually to just drosophilids since other families in the superfamily (Camillidae, Curtonotidae, Diastatidae, Ephydridae) are virtually untreated for Hawaii. Relevant papers not mentioned in either of the two publications are Craddock (1974) on higher relationships, Kaneshiro (1976) on the *planitibia* species-subgroup, and Ohta (1978) on the *grimshawi* species-subgroup.

I have been very critical here because for no other group where adaptive radiation is discussed are the Hawaiian Drosophilidae surpassed in popularity. It is essential that all the details be exact. However, the data in this monograph really is the tip of an iceberg. When culturing methods are devised for most of the species, behavioral geneticists will be able to fine tune the analysis, perhaps down to the level of identifying the neuromuscular channels and genes underlying the sexual fixed-action-patterns. Whether or not that future work (and the recombinant DNA work that will surely ensue) will corroborate Spieths' decisions on behavioral homologies and phylogeny is not most at issue; the fact remains that his observations stimulate questions and lay foundations.—*David Grimaldi, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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